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Dragonfly flight: a Symposium from the 2017 International Congress of Odonatology held at Clare College, Cambridge

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At the 2017 International Congress of Odonatology the opportunity was taken to present a half day symposium on dragonfly flight. This symposium was organised to honour the fundamental contributions to investigations into insect flight made over more than three decades by Charles Ellington, at a Congress being held at his home institution. We were honoured that Charlie was able to attend our Symposium.

Because of a gentleman's agreement with Robin Wootton, dividing up the tasks to be done, Charlie did little direct work on dragonflies. However, his work, especially on unsteady state aerodynamics, has had enormous influence on directing researchers. While he did not *publish* on dragonflies he did think about them a lot and has always been ready to comment and counsel.

In terms of insect flight the four independently controlled wings of dragonflies provides both incredible manoeuvrability and power for the animal, and a supreme test of our capacity for analysis and understanding. Dragonflies can achieve accelerations of greater than 10*g*, and up to 20*g* in some interpretations, linearly as well as in turns. They can brake to a stop within a few wing strokes; two wing strokes can effect a 180° turn, with the animal spinning about its centre of mass. They can hover, with body horizontal. They can fly backwards. They can tumble. They can side-slip, whether climbing, maintaining altitude or diving. And in all these activities they seemingly remain in total control.

In the Symposium the following papers were presented (for multi-authored presentations the presenter's names are underlined):

- Georg Rüppell: Kinematics of dragonfly flight (a commentated video)
- Daran Zheng and <u>Ed Jarzembowski</u>: A brief review of Odonata in mid-Cretaceous Burmese amber
- Esther Appel, Hamed Rajabi and <u>Stanislav Gorb</u>: Structure and properties of dragonfly wings: composite structure of fibrous material supplemented by resilin
- Günther Pass: Insect wings are not "dead" cuticular structures
- Robin Wootton: The flight of Odonata: uniqueness and diversity, answers and questions
- Fritz-Olaf Lehmann: Wing phasing in dragonflies
- <u>Richard Bomphrey</u>, Toshiyuki Nakata, Per Henningsson and Huai-Ti Lin: Flight analysis, aerodynamics, and flight modes

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- Stacey Combes, Susan F. Gagliardi, Mary K. Salcedo, Jay M. Iwasaki, Daniel E. Rundle & James D. Crall: More than one way to capture prey: comparative flight biomechanics and capture strategies of hunting dragonflies
- Dagmar Hilfert-Rüppell and Georg Rüppell: Flight variations in coloured-winged dragonflies (video)

Zheng and Jarzembowski's paper was originally intended to be on the evolution of dragonfly wings, however the opportunity to examine the mid Cretaceous amber fossils from Myanmar was not to be missed. This critical period is during the radiation of both crown group Zygoptera and Anisoptera (and predates such well-known organisms as *Tyrannosaurus rex* by about 50 My!).

For this issue of *The International Journal of Odonatology* papers derived from the presentations are provided.

As he has recently produced a major review covering his contribution Professor Pass declined to produce a further paper, given the danger of self-plagiarism. He refers us to:

> Pass, G. (2018). Beyond aerodynamics: The critical roles of the circulatory and tracheal systems in maintaining insect wing functionality. *Arthropod Structure & Development, 47*, 391–407.
> (open access at https://www.sciencedirect.com/science/article/pii/S1467803918300677).

The papers presented here are:

- **Robin Wootton – Charlie Ellington (1952–2019)** – a career in animal flight mechanics
- **Richard Rowe – History of dragonfly flight**
  From their earliest appearance in the fossil record dragonflies have clearly taken a different approach to flight than other insect groups. Even the superficially similar Neuroptera do not fly like dragonflies. Flight specialisation has enabled dragonflies to occupy a range of niches, as specialised predators of flying insects, for around 300 My.
- **Daran Zheng and Edmund A. Jarzembowski – A brief review of Odonata in mid-Cretaceous Burmese amber**
  Odonatans are rare as amber inclusions, but quite diverse in Cretaceous Burmese amber. In the past two years, over 20 new species have been found by the present authors after studying over 250 odonatans from 300,000 amber inclusions. Most of them have now been published, and here we provide a brief review. Three suborders of crown Odonata have been recorded, including the damselfly families or superfamilies Platycnemididae, Platystictidae, Perilestidae, Hemiphlebiidae, Coenagrionoidea, Pseudostigmatoidea, Mesomegaloprepidae and Dysagrionidae, plus the dragonfly families Lindeniidae, Gomphaeschnidae, Telephlebiidae and Burmaeshnidae, and the damsel-dragonfly family Burmaphlebiidae.
- **Hamed Rajabi and Stas Gorb – How do dragonfly wings work? A brief guide to functional roles of wing structural components**
  Insect wings have no flight muscles, except those situated in the thorax. However, they continuously fine-tune their shapes in response to forces acting during flight. This ability is achieved by the specialised design of the wings and plays a key role in their aerodynamic performance. Dragonfly wings represent an extreme example of this automatic shape control among flying insects. The functionality of the wings results from complex interactions between several structural components of which they are composed. Here we put together the results of our recent works, to review the functional roles of some of the key wing components including vein, membrane, vein microjoint, nodus, basal complex and corrugation. Our results help to understand the relationship between the structure, material and function of each of these wing components. We further use our data to explain how the interactions between the wing components provide dragonflies with fully functional wings.

- **Robin Wootton – Dragonfly flight: morphology, performance and behaviour**
  Odonata flight performance capabilities and behaviour and their body and wing form diversity are explored, and their interrelationships discussed theoretically and from observational evidence. Overall size and particularly wing loading appear predictably to be related to speed range. In Anisoptera at least, relatively short bodies and long wings should favour high speed manoeuvrability, though further information is needed. Medium and low aspect ratio wings are associated with gliding and soaring, but the significance of aspect ratio in flapping flight is less straightforward, and much depends on kinematics. Narrow wing bases, petiolation, basal vein fusion, distal concentration of area and a proximally positioned nodus – described by a newly defined variable, the "nodal index" – all allow high torsion between half-strokes and favour habitually slow flight, while broad wing bases are useful at higher speeds. The "basal complex" in all families seems to be a mechanism for automatic lowering of the trailing edge and maintenance of an effective angle of attack, but the relative merits of different configurations are not yet clear. There is serious need for more quantitative information on a wider range of species and families.
- **Toshiyuki Nakata, Per Henningsson, Huai-Ti Lin and Richard J. Bomphrey – Recent progress on the flight of dragonflies and damselflies**
  Remarkable flight performance is key to the survival of adult Odonata. They integrate varied three-dimensional architectures and kinematics of the wings, unsteady aerodynamics, and sensory feedback control in order to achieve agile flight. Therefore, a diverse range of approaches are necessary to understand their flight strategy comprehensively. Recently, new data have been presented in several key areas in Odonata such as measurement of surface topographies, computational fluid dynamic analyses, quantitative flow visualisation using particle image velocimetry, and optical tracking of free flight trajectories in laboratory environments. In this paper, we briefly review those findings alongside more recent studies that have advanced our understanding of the flight mechanics of Odonata still further.
- **Fritz-Olaf Lehmann and Henja-Niniane Wehmann – Aerodynamic interference depends on stroke plane spacing and wing aspect ratio in damselfly model wings**
  The fluid dynamics of aerodynamic force control in insects depends on how oscillating wings interact with the surrounding air. The resulting flow structures are shaped by the flow induced by the wing's instantaneous motion but also on flow components resulting from force production in previous wing strokes and the motion of other wings flapping in close proximity. In four-winged insects such as damselflies and dragonflies, the flow over the hindwings is affected by the forewing downwash. In these animals, a phase-shift between the stroke cycles of forewing and hindwing modulates aerodynamic performance of the hindwing via leading edge vortex destruction, changes in local flow condition and the wake capture effect. This review is engaged in the significance of wing-wake interference for force control, showing that in damselfly model wings the strength of phase-dependent force modulation critically depends on the vertical spacing between forewing and hindwing stroke planes and the aspect ratio of both wings. We conclude that damselflies and dragonflies reach maximum steering capacity for body posture control when forewings and hindwings flap in close proximity and have similar length. The latter findings are of significance for the evolution and diversification of insect wings because they might explain why forewings and hindwings are little different in the order Odonatoptera.
- **Georg Rüppell and Dagmar Hilfert-Rüppell – Rapid acceleration in Odonata flight: highly inclined and in-phase wing beating**
  Acceleration manoeuvres in free flight in nature of five damselfly (Zygoptera) and four dragonfly (Anisoptera) species were analysed by means of slow motion filming. Changes in stroke frequencies, stroke angles, stroke directions, angles of inclination of the wings, and the phase-relationship of fore- and hindwings were recorded during acceleration. Damselflies

and dragonflies showed similar actions. In rapid acceleration, a shifting of the relationship of the two wing pairs to in-phase stroking and the use of highly inclined wings in the stroke direction opposite to the flight direction can be seen. Slow backward flight was done by phase-shifted stroking, fast backward flight by in-phase stroking. The downstrokes in slow and fast backward flight were quicker than the upstrokes. When fleeing from frogs, dragonflies show extreme flight action: all stroke phases were in-phase and the stroke phases directed toward the frog were very fast and highly inclined. Distances covered per stroke, non-dimensional flight velocities and acceleration are compared and discussed.

As convener of this congress session I thank all the participants for their well-considered and thought-provoking papers. I thank Charlie for travelling to be with us. I thank attendees for the post session gathering where animated discussions continued well into the dusk. I deeply appreciate the efforts of the authors in converting conference presentations into formal journal papers.

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